Title: Forecasting potential routes for movement of endemic birds among important sites for biodiversity in the Albertine Rift under projected climate change.

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Abstract

The ability of species to shift their distributions in response to climate change may be impeded by lack of suitable climate or habitat between species' current and future ranges. We examined the potential for climate and forest cover to limit the movement of bird species among sites of biodiversity importance in the Albertine Rift, East Africa, a biodiversity hotspot. We forecasted future distributions of suitable climate for 12 Albertine Rift endemic bird species using species distribution models based on current climate data and projections of future climate. We used these forecasts alongside contemporary forest cover and natal dispersal estimates to project potential movement of species over time. We identified potentially important pathways for the bird species to move among 30 Important Bird and Biodiversity Areas (IBAs) that are both currently forested and projected to provide suitable climate over intervening time periods. We examined the relative constraints imposed by availability of suitable climate and forest cover on future movements.

The analyses highlighted important pathways of potential dispersal lying along a north-south axis through high elevation areas of the Albertine Rift. Both forest availability and climate suitability were projected to influence bird movement through these landscapes as they are affected by future climate change. Importantly, forest cover and areas projected to contain suitable climate in future were often dissociated in space, which could limit species' responses to climate change. A lack of climatically suitable areas was a far greater impediment to projected movement among IBAs than insufficient forest cover. Although current forest cover appears sufficient to facilitate movement of bird species in this region, protecting the remaining forests in areas also projected to be climatically suitable for species to move through in the future should be a priority for adaptation management.

Keywords:

Bird dispersal, climate change adaptation, connectivity analysis, graph theory, Important Bird and Biodiversity Areas, dispersal corridors, biodiversity conservation, Maximum Entropy.

Introduction

Climate change is driving substantial shifts in species distributions and abundance patterns, and planning for these shifts is a major challenge for conservation biology (Heller and Zavaleta 2009, Parmesan 2006, Stephens, et al. 2016). Of particular concern is the possibility that sites that are currently important for supporting species of conservation concern may not retain suitable climates for these species in the future (Araujo, et al. 2004, Hannah, et al. 2007). There is growing evidence that although many individual sites will experience substantial turnover in species composition as climates change, suitable climate for most species of conservation concern will continue to be represented within networks of conservation sites (Araujo, et al. 2011, Bagchi, et al. 2013, Hole, et al. 2009). There is a strong possibility, however, that in many cases the location of suitable climate will shift to sites other than those where the species currently occur (Araujo, et al. 2011, Bagchi, et al. 2013, Baker, et al. 2015, Hole, et al. 2009). Therefore, the continued effectiveness of site networks at conserving the species for which they were designated will be dependent on the ability of these species to move between sites (Cushman, et al. 2013, Heller and Zavaleta 2009).

Given that species may have to shift their ranges in response to climate change, identifying the dispersal routes they might use between conservation sites, and detecting potential barriers, is an important conservation objective (Aben, et al. 2016, Heller and Zavaleta 2009, Lawler, et al. 2013). The need to identify priority areas for facilitating movement is particularly acute in places that combine high biodiversity and habitat heterogeneity with large and expanding human populations and anthropogenic fragmentation. The Albertine Rift of East Africa is one such region and is widely recognised as a global conservation priority (Brooks, et al. 2001, Brooks, et al. 2006, Plumptre, et al. 2007, Stattersfield, et al. 1998). Climate change is likely to drive considerable turnover in the species in the high elevation areas of the Albertine Rift, and this might particularly disadvantage upper elevation endemics (Garcia, et al. 2012, Hole, et al. 2009) while providing refuge for species for which lower elevations are projected to become climatically unsuitable (Ayebare, et

al. 2013, Garcia, et al. 2012). Climatically, the region has been projected to provide suitable habitat for many species as they shift their ranges (Ayebare, et al. 2013, Hole, et al. 2011), but the rapid rates of forest clearance and fragmentation in the region (Duveiller, et al. 2008, Hole, et al. 2009, Plumptre 2002, Plumptre, et al. 2003, Plumptre, et al. 2007) may impede the ability of species to track suitable future climate. Previous assessments of landscape connectivity in the region have suggested that the majority of conservation sites in the region are currently well interconnected via relatively natural habitat (Plumptre, et al. 2007) and that much of the area connecting sites is projected to be climatically suitable for many species of conservation concern through the 21st century (Ayebare, et al. 2013). However, explicit analyses of animal movement in the context of future climate change and forest cover are needed to identify movement corridors that are robust to breaks in forest cover and narrow areas of unsuitable climate. Emerging techniques for modelling species movement based on graph theory (McRae, et al. 2008) can combine projections of habitat suitability (Lawler, et al. 2013) and species' dispersal ability (see methods) to identify such movement routes and can also compare the relative effects of different limiting factors (e.g. areas with unsuitable climate and gaps in forest cover) on landscape connectivity.

In this study we investigated the potential for 12 endemic forest bird species of the Albertine Rift to move from Important Bird and Biodiversity Areas (IBAs, BirdLife International 2014) that are currently climatically suitable to those that are projected to be suitable in the future. IBAs are identified using standardised criteria based on the presence of species of conservation concern and networks of these sites provide a useful framework for evaluating the extent to which sites of biodiversity importance might be connected under future scenarios of environmental change. Previous analyses of African IBAs have indicated that they will remain important for bird species of conservation concern under future climate change, but that there will potentially be substantial turnover in the species that individual IBAs are climatically suitable for (Baker, et al. 2015, Hole, et al. 2009). In our analyses we combined species distribution modelling with two methods for assessing connectivity (shortest paths and current flow), to identify areas that might be important for

96 movement of these species in response to climate change up to 2100. We accounted for both the
97 current distribution of forest and the projected future climate suitability of IBAs and the intervening
98 landscape. We explicitly incorporated estimates of species' dispersal ability in our analyses by
99 allowing movement between non-adjacent cells in the landscape that are within each species' natal
100 dispersal range. We used these analyses to address the following two questions: 1) Will a lack of
101 availability of areas of suitable climate or a lack of forest pose the greater barrier to species
102 movement between IBAs? 2) Which routes are projected to be most important for species
103 movement from IBAs that are currently climatically suitable to those that are projected to be
104 suitable in the future?

105 # Methods

106 ### *Study region*

107 The Albertine Rift region is part of the Eastern Afromontane Biodiversity Hotspot
108 (Mittermeier, et al. 2004) and is one of the most topographically and ecologically diverse areas of
109 Africa. It supports 52% of the bird species of continental Africa, including 42 species endemic to the
110 region (Plumptre, et al. 2003 report 41 species but this increases according to revised taxonomy
111 available at www.birdlife.org/datazone/info/taxonomy). It also supports one of the highest rural
112 human populations in Africa with an average population density of 94.6 people per km^2, rising to
113 600-700 people per km^2 in some areas (Burgess, et al. 2007, Plumptre, et al. 2003).

114 This study is centred on the Albertine Rift Mountains Endemic Bird Area (EBA), which covers
115 approximately 56,000 km^2 and includes the mountains that flank the Albertine Rift Valley, from the
116 Lendu Plateau in northeast Democratic Republic of the Congo (DRC), south to the Marungu
117 Highlands also in DRC, plus the mountains of south-west Uganda, Rwanda, Burundi and extreme
118 western Tanzania (Figure 1)**.** In order to include potential future range shifts of our study species, we
119 also included areas outside the Albertine Rift Mountains EBA, including part of the adjacent Eastern
120 Zairean Lowlands EBA (Okapi Faunal Reserve and Mount Hoyo Reserve in the North, Maiko to the

West and the Itombwe Mountains in the South) because birds could conceivably move through or establish in these adjacent regions even if they do not currently occur there.

Data sets

Bird locality records

The data set used in this study was compiled from field surveys to assess the biodiversity of the Albertine Rift Forests undertaken between 1999 and 2007 throughout the region by the Wildlife Conservation Society (A. J. Plumptre, unpublished data; Ayebare, et al. 2013). Five-minute point counts were made at 250 m intervals along randomly placed transects in sectors of the forests or, in the case of remote and very rugged areas, along reconnaissance walks which aimed to follow specific compass directions but avoid major obstacles to the team's progress. The surveys targeted the coverage of as much of the forest as possible, particularly the full altitude range found at a site. Presence of armed groups in eastern Democratic Republic of Congo made it impossible to sample all sites planned but this will not have affected estimates of the niche envelopes calculated for this paper. At each point the ornithological team would wait for two minutes to allow birds to settle down and then start the point count during which all birds seen or heard were recorded.

We used data from these surveys for 12 of the 42 restricted-range bird species entirely confined to the Albertine Rift mountains Endemic Bird Area (Plumptre, et al. 2003, Stattersfield, et al. 1998). These 12 species (listed in Table 1) were chosen as: i) representative of the broader set of Albertine Rift endemics, including some which are common and widespread and others which are rare (or rarely recorded) and/or which are confined to only part of the region and ii) species with more than 10 locality records (those with 10 or fewer records were excluded as they could not be modelled robustly). Moist montane forest is the main habitat type for all species (Table 1).

Dispersal data

Estimates of the mean and maximum natal dispersal distances for these species were obtained from BirdLife's and IUCN's Species Information Service database (BirdLife International,

146 unpublished data). The database contains banded estimates for each genus for mean and maximum
147 natal dispersal distance, based on species-specific estimates from the literature, with data gaps filled
148 by extrapolation from close relatives. All species used in this study belonged to genera with mean
149 and maximum natal dispersal distance bands of 0-4, 5-24, or 25-49 km (Table 1). We used the mid-
150 point of the mean dispersal band and the upper limit of the maximum dispersal band as estimates of
151 mean and maximum dispersal respectively.

152 *Climate and environmental data*

153 We used seven environmental variables to model the distributions of the 12 study species.
154 These variables were i) mean temperature of the warmest month; ii) mean temperature of the
155 coldest month; iii) the ratio of actual to potential evapotranspiration; iv) wet season intensity; v) dry
156 season intensity; vi) slope; vii) aspect. These variables have proved optimal for modelling a wide
157 range of bird species across Africa (Hole et al, 2009). Variables (i) through (v) were obtained for the
158 period 1950 – 2000 (hereafter referred to as 20th Century) from Worldclim
159 (http://www.worldclim.org/) at 30" (arc second; approximately 1 km^2 at the equator) resolution. We
160 used a 30" resolution because it was the finest resolution available for the environmental variables
161 we used and a fine resolution is appropriate for modelling distributions in areas with high
162 topographic complexity like the Albertine Rift. Slope and aspect were taken from the Global Agro-
163 Ecological Zones database (Fischer, et al. 2008) and were selected to capture the fine scale
164 topography within the region and the resultant impacts on local climate. Projections of future
165 climate variables were obtained from three General Circulation Models (GCMs), GFDL CM2.1,
166 ECHAM5-OM and HadGEM1, over three time periods (2011-2040, 2041 – 2070 and 2071 – 2100,
167 hereafter referred to by their midpoints: 2025, 2055 and 2085) and for the A1B SRES scenario
168 (approximately equivalent to RCP 6.0 in the IPCC's Fifth Assessment Report). GCM outputs were
169 downscaled using the change factor approach (Tabor and Williams 2010, Wilby, et al. 2004) to 30".

Forest cover data

Land cover classification was based on the Globcover 2009 database (Arino 2010). Data were obtained for the Albertine Rift region at a 30'' resolution (see Figure 2). We initially considered all cells categorised in Globcover 2009 as "closed to open broad-leaved evergreen" or "semi-deciduous forest and closed broad-leaved deciduous forest" (categories 40 and 50 in Globcover 2009) as forested; all other cells were classified as non-forested. We then refined these maps using supplemental regional satellite imagery and regional forest maps (see Ayebare, et al. 2013) to reclassify plantations, often classified as natural forest by Globcover 2009, as non-forest cells.

Analytical methodology

We compared the relative contributions of forest cover and climate suitability on bird movement and projected potential movement routes for each of the 12 species through the multi-stage analysis detailed below and summarised in Figure 2.

Species distribution models and projections of suitable climate

Species distribution models were developed by modelling the locality records of the 12 species as functions of the seven environmental variables using a commonly applied maximum entropy approach, MaxEnt (Phillips, et al. 2006, Phillips and Dudík 2008). To reduce sampling bias of background points we constrained the model to select background points only from within the Albertine Rift EBA (Stattersfield, et al. 1998). We tested the predictive ability of each model using the values obtained for the area under the curve (AUC) of a receiver operating characteristic plot (Hanley and McNeil 1982), with each model calibrated on a random selection of 70% of the observation data, and projection accuracy evaluated on the remaining 30%.

The MaxEnt model for each species was used to project the climatic suitability of each 30'' cell, for that species, in the 20th century (using the observed climate data) and for the three future time periods (using the downscaled GCM projections for the corresponding period). Climatic suitability for each cell ranged between 0 and 1, with each GCM leading to different projections of

climatic suitability. Hence, we used the mean of the three GCM projections for each time period as a measure of the climatic suitability of a cell. We also calculated the minimum of the mean climatic suitability of each cell for each pair of consecutive time periods (i.e. between (i) 20th century and 2025; (ii) 2025 and 2055 and; (iii) 2055 and 2085), which we used as a stringent measure of climate suitability of each cell during each pair of time periods. This enabled the identification of routes likely to remain climatically suitable throughout the entire period being considered.

Habitat suitability

Habitat suitability for the forest birds considered in this study will depend on both suitable climate and forest availability. Movement among IBAs will therefore be restricted when the availability of either suitable climate or forest is limited in the areas between them. In our connectivity analyses we estimated the relative contributions that gaps in forest cover or suitable climate might make on the movement of birds among IBAs in the future by comparing movement under four limitation regimes that differed in how the habitat suitability of each grid square was calculated. The four regimes were: 1) no limitation (a null model), where habitat suitability of all cells was set to the maximum current climatic suitability for that species across the study region; 2) climate-only limitation, where habitat suitability was set as the projected climatic suitability of each cell; 3) forest-only limitation, where habitat suitability was defined purely on the basis of whether a cell was either forested (habitat suitability was set to the maximum current climatic suitability for that species across the study region) or not (habitat suitability was set to 0); and 4) climate-and-forest co-limitation, where the habitat suitability of each cell was set to zero if it was not forested or equal to the projected climatic suitability of that cell otherwise. These 30" habitat suitability cells were aggregated by averaging to either a 5 x 5 km (2.5', arc minute) resolution for six poor dispersing species (max dispersal 5 – 24.9 km, see Table 1) or 10 x 10 km (5') resolution for the six other species with better dispersal ability (max dispersal 25 – 49.9 km). Computer run times and memory requirements meant it was not possible to perform all analyses at finer resolutions for all

220 species but previous studies (Ayebare, et al. 2013, McRae, et al. 2008) suggest that connectivity
221 analyses are generally robust to such small changes in grid cell resolution.

222 *Connectivity analyses*

223 We used two contrasting methods to identify possible routes of species movement among
224 IBAs; "shortest paths" and "current flow". Both methods are based in graph theory (Cushman, et al.
225 2013, McRae, et al. 2008) and account for the "conductance" of each cell traversed on the route
226 between the origin and the destination. The conductance of a cell can be thought of as the inverse
227 of the cost of travelling through it (McRae, et al. 2008). The shortest path (also referred to as least-
228 cost path) between the origin and the destination follows the route with the smallest cumulative
229 cost (i.e. the sum of the costs of all cells traversed along the route is minimised). This provides an
230 estimate of the best route between the source and destination. Potential drawbacks of using
231 shortest paths are that individuals are unlikely to follow a single, optimal route (McRae, et al. 2008)
232 and several different routes might, together, allow greater movement of individuals (McRae, et al.
233 2008, Phillips, et al. 2008). Recently, methods have been developed that consider movement of
234 individuals along multiple pathways (Carroll, et al. 2012, McRae, et al. 2008, Phillips, et al. 2008).
235 One such approach, current flow, likens the movement of individuals through landscapes to the flow
236 of current through electrical circuits (Carroll, et al. 2012, McRae, et al. 2008, van Etten and Hijmans
237 2010). This approach allows for efficient calculation, for each cell, of the probability that a random
238 walker will move through it while moving from an origin to a destination. This probability provides a
239 measure of how important the cell is for movement between the origin and destination when
240 knowledge of the landscape is limited to cells that can be reached in one dispersal event.

241 To estimate the shortest paths and current flow we calculated a conductance matrix for the
242 landscape. This matrix contains information on the ability of individuals to move between each pair
243 of cells in the landscape: zero conductance indicates that it is impossible for individuals to move
244 directly between the cells while large conductance values indicate that there is little impediment to

movement between them. In our analyses, the conductance between pairs of cells (G_{ijk}) was defined as

$$G_{ijk} = \frac{d_{ijk}}{-\log_e(\sqrt{p_{ik}\, p_{jk}})} \quad \text{(eq. 1)}$$

where p_{ik} is the habitat suitability of each cell i for species k. The denominator is analogous to the definition of cost used by Graham *et al.* (2010). The numerator, d_{ijk} is the dispersal potential of species k between cells i and j and was estimated according to a truncated negative exponential dispersal function so that

$$d_{ijk} = \begin{cases} \frac{\exp\left(-\frac{r_{ij}}{\lambda_k}\right)}{\lambda_k}, & r_{ij} < \lambda_{max_k} \\ 0, & r_{ij} > \lambda_{max_k} \end{cases} \quad \text{(eq. 2)}$$

where r_{ij} is the distance between cells i and j, and λ_k and λ_{max_k} are estimates of the mean and maximum natal dispersal distances for species k respectively (see Table 1). No direct dispersal was allowed between cells that were further apart than the maximum observed natal dispersal of each species. This formulation allowed individuals to move directly to non-neighbouring cells within their maximum natal dispersal distance without having to pass through the intervening ones. This is useful because individuals are likely to be able to cross mosaic habitats and narrow areas of unsuitable habitat. Note that the dispersal function above penalised movement over longer distances so that skipping intermediate cells would not automatically reduce the cost of a route. This formulation of dispersal constrained the distance travelled by individuals at each dispersal event. Routes that traversed wide areas of unsuitable habitat, relative to the dispersal ability of the species, were penalized by the dispersal function. As a result, the relative suitability of alternative routes was increased. Our approach did not quantify the time it would take for a population to expand into new areas.

The IBAs cover multiple 10 x 10 km (and 5 x 5 km) cells, so we calculated the routes between the centroids of the IBA polygons. The conductance between cells within the source and destination IBAs was set very high (G_{ijk} = 1000, several times higher than the highest values otherwise observed). Therefore, the cost of movement between two IBAs is composed principally of the cost of movement between their boundaries.

Once the conductance matrices had been computed, we used the gdistance package (van Etten 2011) in R 3.2.3 (R Development Core Team 2015) to compute the shortest paths and the current flow between each pair of IBAs, for each species and under each of the four limitation regimes (null, climate-only, forest-only and climate-and-forest co-limitation). We also calculated the length of the shortest path and the resistance distance of the current flow (see McRae, et al. 2008, for a definition) associated with movement of each species between each pair of IBAs. We hereafter refer to both the length of shortest path and the resistance distance of the current flow as path length.

Quantifying path importance

We assumed that birds are most likely to move from IBAs that are projected to decline in suitability for a species to IBAs projected to provide suitable future climate. To represent this expectation, we adjusted the potential importance of the connections between each pair of IBAs to account for climatic change by calculating the difference in mean climatic suitability between the beginning and end of each time period within the source IBA and multiplying this by the future mean suitability of each potential destination IBA. This measure of importance was set to zero for pairs where the mean suitability of a source IBA remained the same or increased (i.e. there would be no reason for the species to move).

Models of path length

To quantify the potential for unsuitable climate and gaps in forest cover to limit movement of each species among IBAs, we divided the path lengths under three of the limitation regimes

(climate-only, forest-only, and climate-and-forest) by the path length under the null regime, for every source and destination IBA combination. We then modelled these (log-transformed) ratios (shortest path and current flow distances were modelled separately) as a function of limitation regime using linear mixed-effects models with species, source IBA and destination IBA entered as random effects. The path importance (described in the previous section) between each pair of IBAs for each species was included as a weights argument in the model.

Forecasting routes for bird movement

Using the results from the shortest path and current flow analyses separately, we estimated the importance of a cell for each species' movements as the weighted mean (across all pairs of IBAs, weighted by the importance of the IBA pair) of the number of paths traversing that cell. This represents the proportion of journeys predicted to traverse that cell, and varies from 0 (no paths pass through the cell) to 1 (all paths with non-zero importance pass through them). We reduced the resolution of the results from the six poor-dispersing species that were modelled at a 5 x 5 km grid size (*A. personata*, *B. diops*, *P. nobilis*, *K. rufocinctus*, *O. ruwenzorii* and *P. fasciiventer*) by calculating the mean proportion of shortest paths (and current flow) across the four cells in each 10 x 10 km grid cell. Finally, we calculated the mean of the proportion of shortest paths and (separately) current flow passing through each cell across all species for each of the four limitation regimes and three time periods. The finite dimensions of the study area and the locations of the IBAs mean that some cells are more likely to be used for movement purely due to their location. We corrected for this, both for the shortest paths and current flow methods, by subtracting the results for each cell under the null limitation regime from those obtained under the other three regimes. Cells with negative difference values were set to zero (i.e. these cells were considered to have no role in movement among IBAs). The corrected estimates of movement from the shortest path and current flow methods were then plotted separately for each time period to identify the most important dispersal routes among IBAs.

Results

MaxEnt model performance

The number of locality records per species ranged from 18 for *Z. tanganjicae* to 468 for *A. personata* (median = 105.5, IQR = 150; Table 1). Model fit for individual species distribution models, assessed using AUC, ranged from 0.818 to 0.919 (median = 0.885; IQR = 0.073; Table 1), indicating good model performance for all 12 species.

Changes in climate suitability

Overall, the species distribution models projected that availability of climatically suitable habitat in the region will decline by the end of the 21st Century (Figure 3a). The models forecasted that, throughout the current century, the high elevation areas along the Albertine Rift will provide the most suitable future climate for the majority of species considered here (Figure 3a). These areas were reasonably well forested in the early 21st Century: of the area projected to be suitable for at least one species at the end of the century, about 50% was classified as forested (Figure 3b). In contrast, only 33% of the area that was projected as climatically unsuitable for all 12 species was classified as forest. The western part of the region retained the most forest cover (Figure 3b). This area included the foothills of the western cordillera of the Albertine Rift and hence was generally lower-lying and less climatically suitable for the suite of species considered here.

Connectivity analyses

Models of path lengths

The mixed-effects models suggested that climate will strongly limit the movement among IBAs of the birds of the Albertine Rift endemics considered here. This is indicated by the large increases in the path lengths of both the shortest paths (c.73 -fold increase) and current flow (c. 113-fold increase), between the null regime and climate-limitation regime (Figure 4). Restricting movement to currently forested areas, without considering climate limits, resulted in a much smaller

increase in path lengths compared to the null regime, although the increase was still substantial (c. 10-fold increase in shortest path lengths and c. 37-fold increase in current flow path lengths). The combined effects of movements being restricted by both climate suitability and forest occurrence led to only a slight increase in path length from that expected in the climate-only limitation regime (c. 1.5-fold increase in shortest path lengths and c. 1.6-fold increase in current flow path lengths). The effects of limitation regimes were consistent across the three time periods (Figure 4).

Forecasts of routes for bird movement

Shortest paths (Figure 5a) were less diffuse than current flow (Figure 5b) but both methods predicted that movement would be concentrated in broadly similar areas under a given limitation regime. Figure 5 presents the results for the central time period centred on 2055, but the results for the other time periods were very similar (See Supplementary Figures S1 and S2). The extensive forest cover and suitable climate along the western ridge of the rift meant that this area supported the densest concentration of shortest paths and current flow under all limitation regimes, and this region also encompasses several large IBAs. In particular, the areas encompassing and connecting the Itombwe Mountains, eastern reaches of Kahuzi-Biega NP, Volcans NP and Ruwenzori mountains had very high densities of paths regardless of analytical approach or limitation regime.

There were important differences in projected path densities among limitation regimes. Under the forest-only limitation regime, the greatest concentration of shortest paths and, in particular, current flow, shifted towards the forested western part of the region (Figure 5, left panels). In contrast, when climate was the sole factor limiting movement among IBAs, the highest concentrations of shortest paths and current flow were situated in the centre of the region, following a north-south axis along the high elevation areas of the Albertine Rift (Figure 5, middle panels). When only climate was limiting, both the shortest path and current flow analyses suggested that the eastern shore of Lake Kivu, running northwards from Nyungwe Forest to Volcans and Virunga National Parks (NP), would be important for bird movement. However, a lack of forest in the

366 area reduced its projected importance for bird movement under the co-limitation regime (Figure 5,
367 right panels).

368 Discussion

369 The species distribution models projected that the high elevation areas of the Albertine Rift
370 will provide the most suitable climate for most of the species considered here. Given projected
371 climate change in the Albertine Rift and assuming no loss of the forest cover available in the early
372 21st Century, our analyses suggested that limited availability of suitable climate, rather than gaps in
373 forest cover, will impose the greatest constraints on movement among IBAs. Despite these
374 constraints, our analyses identified several movement corridors and suggested that the well-
375 forested, high-elevation areas along the western flank of the Albertine Rift will be particularly
376 important for the 12 species as they adjust their ranges in response to climate change.

377 A single important route through the central high elevation areas of the region connected a
378 large proportion of the IBAs included in our analyses. This route runs along a north-south axis from
379 the Itombwe Mountains through the high elevation areas of Kahuzi-Beiga NP, before passing
380 through the "Greater Virunga Landscape" (incorporating Volcans NP, Virunga NP, Queen Elizabeth
381 NP, Rwenzori NP and Semiliki NP among others; Plumptre, et al. 2007). The Itombwe Mountains,
382 parts of Virunga NP and the Rwenzori Mountains were particularly important locations on this route.
383 Both the Greater Virunga Landscape and the Itombwe Mountains have been previously highlighted
384 as among the most biodiverse regions in Africa (Hart, et al. 1999, Plumptre, et al. 2007), and the
385 evidence from our analyses of their potential role in maintaining the future connectivity of the
386 region provides further support for their high conservation value.

387 A previous analysis of conservation priorities in the region (but not in a climate change
388 context) highlighted six main areas as crucial for connecting the conservation site network in the
389 Albertine Rift (Plumptre, et al. 2007). The Greater Virunga Landscape was one of these areas, and, as
390 discussed above, it is also identified by our analyses. Three other areas considered by Plumptre *et al*.

391 (2007) also lie within the scope of this study (the other two are either too small or lie outside of the
392 region we consider). These areas are (i) between Murchison Falls and Semliki Reserves, (ii) from
393 Maiko NP through Kahuzi-Beiga NP to the Itombwe Mountains and (iii) from Mount Kabobo to the
394 Marungu Highlands at the southern extremity of the region. Under the forest-only limitation regime,
395 high densities of paths occurred through all three areas. However, the future climates along the
396 forested routes through two of these areas (i and iii) were projected to be unsuitable for the species
397 considered here, and consequently these areas were less important for bird movement under the
398 climate-only and co-limitation regimes. The highland route between eastern Kahuzi-Beiga and the
399 Itombwe mountains (area ii) is forested and the future climate is projected to be suitable for the
400 species included in this study, emphasising the likely importance of forested, high-elevation routes in
401 this region. The lower elevation forest routes identified by Plumptre *et al.* (2007) may continue to be
402 important for species that are tolerant of a wide range of climates. However, for the landscape to
403 allow movement of this suite of 12 endemic bird species under climate change, relatively continuous
404 forest must be maintained in the climatically suitable highlands of the region.

405 Although our analyses suggested that, in future, forest cover will be generally less limiting to
406 bird movement than availability of suitable climate, movement through some areas projected to be
407 climatically suitable was constrained by a lack of forest cover. The most important of these forest-
408 limited connections is along the eastern shore of Lake Kivu between Nyungwe Forest and Volcans NP
409 to its north. Under the climate-only regime, this route appeared very important and may also have
410 facilitated movement further north of Volcans NP, through Echuya Forest Reserve and Bwindi
411 Impenetrable NP to the eastern edge of Queen Elizabeth NP. However, much of the forest between
412 Nyungwe Forest and Volcans NP has been converted to *Eucalyptus* plantations. Consequently, the
413 path density along this route decreased substantially once gaps in forest cover were accounted for.

414 It should be recognised that the inference that bird movement will be constrained more by
415 climate than by forest cover, is dependent on there being no further forest loss in the region,

especially along the high ground flanking the west of the Albertine Rift Valley where suitable climate and forest cover coincide. Forest cover and suitable projected climate overlap little beyond the western ridge of the Albertine Rift, and hence, loss of these high-elevation forests could greatly impede bird movement across the region. However, the high human population density and prevalence of armed conflict have driven rapid and extensive forest loss across the region, especially outside protected areas (Duveiller, et al. 2008, Hanson, et al. 2009, Kanyamibwa 1998, Plumptre, et al. 2003). Areas that our analyses highlighted as especially important for bird movement along the western Albertine rift, like Virunga NP and the Itombwe Mountains, have also suffered recent deforestation (Hanson, et al. 2009, Hart, et al. 1999, McNeely 2003, Plumptre, et al. 2003). In addition, human responses to climate change in the region may well lead to changes in where people live, where they cultivate land, and how they generate energy, all of which could have substantial impacts on deforestation. Such indirect impacts of climate change may prove to be as significant as direct impacts (Segan, et al. 2015). It is unclear how much further forest destruction the region can undergo before forest becomes more of a limiting factor than climate in the response of the endemic forest birds to climate change. Ideally, we would have incorporated projections of forest loss (which are available for some tropical areas, e.g. Soares-Filho, et al. 2006) into our analyses. Projections of deforestation would have allowed us to identify movement corridors that are likely to remain forested and suggest areas that could be prioritised for additional protection. Unfortunately, reliable projections of deforestation are currently unavailable for the region, largely because human activity is likely to be the primary driver but is also highly uncertain (Ayebare, et al. 2013). What is almost certain however, is that incorporating future deforestation scenarios in our models would have increased the projected constraints on future range shifts by the bird species we considered.

The use of methods from graph theory to model animal movement, as we do in this study, provides a powerful tool for ecologists and conservation biologists (Lawler, et al. 2013, McRae, et al. 2008). Nevertheless, such approaches are inevitably simplifications of complex ecological processes

(Moilanen 2011, Sawyer, et al. 2011). In particular, our analyses ignored variation within populations in dispersal ability, behaviour and habitat requirements and the capacity for populations to adapt evolutionarily in response to environmental change (Baguette and Van Dyck 2007, Hawkes 2009, Nussey, et al. 2005). It is unclear how such simplifications might affect the analyses. One criticism of some movement analyses has been their inability to allow individuals to cross even relatively small sections of unsuitable habitat (Moilanen 2011). Although the data we used to parameterise the dispersal functions in our analyses were relatively crude and ignored variation among individuals, their inclusion in the modelling framework enhanced biological realism by allowing small patches of suitable habitat to serve as stepping stones to areas that might sustain viable populations. This approach could be developed further, perhaps in combination with more extensive dispersal information. Another parameter that is very difficult to measure is the scale at which individuals perceive and respond to the landscape they are moving through. In this study, we compared two methods that make contrasting assumptions about perception. Shortest paths assume a perfect knowledge of the landscape (so individuals always take the most direct route) while current-flow paths assume individuals have no knowledge of the wider landscape beyond their next move (so individuals take a more circuitous route). Although the current-flow method resulted in more diffuse movement routes than the shortest path method, both highlighted the same areas as most important and suggested similar differences among limitation regimes. Thus, it appears that our main conclusions were not sensitive to assumptions about bird perception.

More refined forest classification data and climate projections would also have improved our analyses. We used forest classification data based on satellite images (Arino 2010) that provide consistent classifications across large spatial scales (Sawyer, et al. 2011). However, the bird species considered here probably have more specialised habitat preferences than can be defined using current remotely-sensed images. Although we augmented the forest classification data from GlobCover 2009 (Arino 2010) by reclassifying known plantations as unsuitable habitat, our models undoubtedly allowed movement through unsuitable forest and prevented movement through

suitable forests. Similar concerns could be raised about the projections of future climate from the species distribution models, because although they provide an efficient means of estimating conductance across large landscapes for multiple species (Lawler, et al. 2013), they undoubtedly include errors. Such errors will shift the projected movement corridors and could also alter the estimates of path lengths. In particular, if the distribution of suitable future climate is less restricted than is projected by our species distribution models, the relative contribution of forest cover to movement of these species could increase.

Overall, our analyses suggest that there are corridors of both suitable climate and forest cover within the Albertine Rift region that will permit the region's endemic forest bird species to move in response to future climate change. However, corridors defined by considering either climate or forest cover alone may prove inappropriate or inadequate, and so, both should be considered in conservation planning. Although movement of birds in our models was far more limited by the availability of suitable climate than by forest cover, this assumed no loss of current forest cover, which is unrealistically optimistic. Therefore, although the existence of movement corridors that endemic birds might use to respond to shifting climate provides hope for conservation adaptation to climate change in the Albertine Rift, implementing a landscape-scale conservation strategy to cope with climate change faces considerable challenges in this biodiversity hotspot.

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599

Tables

Table 1: Restricted-range bird species endemic to the Albertine Rift included in the analysis, indicating their 2016 IUCN Red List category (LC: Least Concern; NT: Near Threatened), mean and maximum dispersal distance bands (representing the mean for each genus or, where indicated with asterisks, for each family) and preferred habitat. The number of point localities where the species was observed and used in the species distribution models and the predictive performance of the models (measured by AUC) are also presented.

Species	Red List category	Mean dispersal band (km)	Max dispersal band (km)	Preferred Habitat	No. of point localities observed	Test AUC
Alethe poliophrys	LC	5-24*	25-49*	Moist montane forest	95	0.820
Apalis personata	LC	5-24	5-24	Moist montane forest	468	0.865
Batis diops	LC	0-4	0-4	Moist and dry montane forest	162	0.904
Pternistis nobilis	LC	5-24	5-24	Moist montane forest and shrubland	24	0.911
Hemitesia neumanni	LC	5-24	25-49	Moist montane forest	101	0.892
Kupeornis rufocinctus	NT	0-4	5-24	Moist montane forest	25	0.865
Nectarinia alinae	LC	5-24	25-49	Moist montane forest	110	0.818
Nectarinia purpureiventris	LC	5-24	25-49	Moist montane forest	121	0.872

Nectarinia regia	LC	5-24	25-49	Moist montane forest	300	0.919
Oreolais ruwenzorii	LC	0-4*	5-24*	Moist Montane Forest	448	0.887
Parus fasciiventer	LC	0-4	5-24	Moist Montane Forest	54	0.885
Zoothera tanganjicae	NT	5-24	25-49	Moist Montane Forest	18	0.884

607

608 # Figures Legends

609 **Figure 1:** Map of the Albertine Rift study region with the locations of the 30 IBAs considered. The
610 abbreviation "NP" stands for National Park. Elevation (background shading), large lakes (blue fill and
611 text) and international borders (dotted and dashed lines) are also indicated.

612 **Figure 2:** Schematic outline of the analysis. White boxes and black arrows indicate steps that were
613 used to address both questions while grey boxes and lines indicate steps only used to address
614 question 1 and blue boxes and arrows indicate steps only used to address question 2. See the text
615 for more details.

616 **Figure 3:** Maps of the Albertine Rift presenting (a) summed projected climate suitability for the 12
617 bird species for the time periods centred on 2025, 2055 and 2085 and (b) early 21st century forest
618 cover based on Globcover 2009 (Arino 2010) and adjusted to account for known plantations. Dark
619 blue lines indicate IBA boundaries.

620 **Figure 4**: A comparison of path lengths resulting from the three limitation regimes using (a) shortest
621 paths and (b) current flow to model movement of 12 Albertine Rift endemic bird species in the time
622 period centred on 2055 (there was little variation among time periods in path lengths). Points
623 represent the mean ratio of path lengths (dimensionless) under each regime to the path length
624 under the null regime (i.e. no limitation by either forest or climate). Larger values indicate greater
625 limitation. Error bars represent the standard-errors of the mean.

626 **Figure 5:** Maps of (a) shortest paths and (b) current flow summed across all pairs of IBAs and species
627 for the three limitation regimes in the time period centred on 2055 (similar results were obtained for
628 the other time periods). For each species and method, we calculated the proportion of paths that
629 ran through each cell under each limitation regime. We subtracted the proportion of paths
630 traversing cells under the null limitation regime from each of the other three limitation regimes. We
631 then averaged these proportions across species to get a measure of the proportion of paths across

all 12 species that traversed each cell. White areas indicate cells with no paths. Black polygons indicate the IBA boundaries.

Figure S1: Maps of shortest paths summed across all pairs of IBAs and species for the three limitation regimes presented separately for all three time periods considered. For each species and method, we calculated the proportion of paths that ran through each cell. The proportion of paths has been corrected by subtracting the proportion of paths traversing cells under the null limitation regime. The corrected proportions were then averaged across species to get a measure of the proportion of paths across all 12 species that traversed each cell. White areas indicate cells traversed by no paths. Black polygons indicate the IBA boundaries.

Figure S2: The proportion of current flow, from all pairs of IBAs and species, traversing each cell under the three limitation regimes for all three time periods. For each species, method and limitation regime, we calculated the proportion of paths that ran through each cell. The proportion of paths was corrected by subtracting the proportion of paths traversing cells under the null limitation regime. Cells that were not used by any species between any pair of IBAs get values of 0 (white). The black polygons indicate the IBA boundaries.

Figure S3: Maps of 2055 shortest paths for each species and limitation regime separately, summed across all pairs of IBAs. For each species and method, we calculated the proportion of paths that ran through each cell. The proportion of paths has been corrected by subtracting the proportion of paths traversing cells under the null limitation regime. The data from all species are presented on the same common scale. White areas had no paths passing through them. Black polygons indicate the IBA boundaries.

Figure S4: Maps of 2055 current flow for each species and limitation regime separately, summed across all pairs of IBAs. For each species and method, we calculated the proportion of paths that ran through each cell. The proportion of paths was corrected by subtracting the proportion of paths

traversing cells under the null limitation regime. The data from all species are presented on a common scale. White areas had no paths passing through them. Black polygons indicate the IBA boundaries.